Distribution, Activity, and Food Habits of Juvenile *Tegula funebralis* and *Littorina scutulata* (Gastropoda : Prosobranchia) as they Relate to Resource Partitioning

BY

JEFFREY T. JENSEN

Hopkins Marine Station of Stanford University, Pacific Grove, California 93950

(4 Text figures)

INTRODUCTION

The snails *Tegula funebralis* A. Adams, 1853 and *Littorina scutulata* Gould, 1849 are abundant in the mid-tide zone on California rocky shores. Numerous studies have been made on the adults of *T. funebralis* (see Veliger, 6, suppl., 1964; and Abbott & Haderlie, 1980), but the juveniles have received comparatively little attention. *Littorina scutulata* has also been studied (see review in Abbott & Haderlie, *op. cit.*), and the possibility exists that two distinct forms or species are involved (Murray, 1979), but many aspects of the natural history are still incompletely known. No previous studies have focused primarily on the juveniles of either *T. funebralis* or *L. scutulata,* particularly on their relationship to one another in the middle intertidal zone community. The present work examines the possibility of competitive resource partitioning interactions between the young of these herbivorous gastropods by comparing their distribution, activity patterns, and food habits.

DISTRIBUTION and MOVEMENTS

For present purposes juvenile snails are defined as those individuals measuring 4 mm or less in maximum linear shell dimension. All studies were conducted on Mussel Point, Pacific Grove, California, adjacent to the Hopkins Marine Station, in a region protected from strong wave action. The 4 sites chosen all displayed sloping rocks showing marked vertical zonation and a diversity of habitats including bare granite, surfaces covered with barnacles or algae, and some small pools and cracks where sand could accumulate. At each site a vertical transect was extended from a 0.0 m level upward, and two 25 cm^2 samples were taken at each 15 cm increment in height above mean lower low water. Absolute height was determined from a surveyed benchmark nearby. At each level the 25 cm^2 quadrats were placed a variable distance from the middle of the transect on the basis of random numbers. All *Littorina* and *Tegula* were inspected in each quadrat, and field records made of the 22 distinct microhabitats occupied by the snails as they were collected. Holdfasts and fronds of algae were removed from the quadrat and examined separately. In all situations where accurate counts could not be made in the field, samples were bagged and examined later under a dissecting microscope.

The 4 transects sampled showed consistent trends; pooled data appear in Figure 1. In vertical placements, juvenile *Tegula funebralis* occurred predominantly below the +1.2 m level, while juvenile *Littorina scutulata* were found mostly above the +0.9 m level, the two populations overlapping mainly 0.9-1.2 m above MLLW. Figure 1 shows distribution of the snails according to specific microhabitat, with habitats (A-V) arranged in a sequence to show the shifting relative abundance of the two species. Young *Tegula funebralis* are seen to occur chiefly in sandy holdfasts of the common macroalgae (e.g., *Rhodoglossum affine* (Harvey) Kylin, 1928) and in rocky crevices, while *Littorina scutulata* are more frequently on the fronds of the same macroalgae and in empty barnacle shells. Thus, microhabitat partitioning and zonation sharply limit the possible interactions between juveniles of the two species.

These data on vertical placement and habitat of small

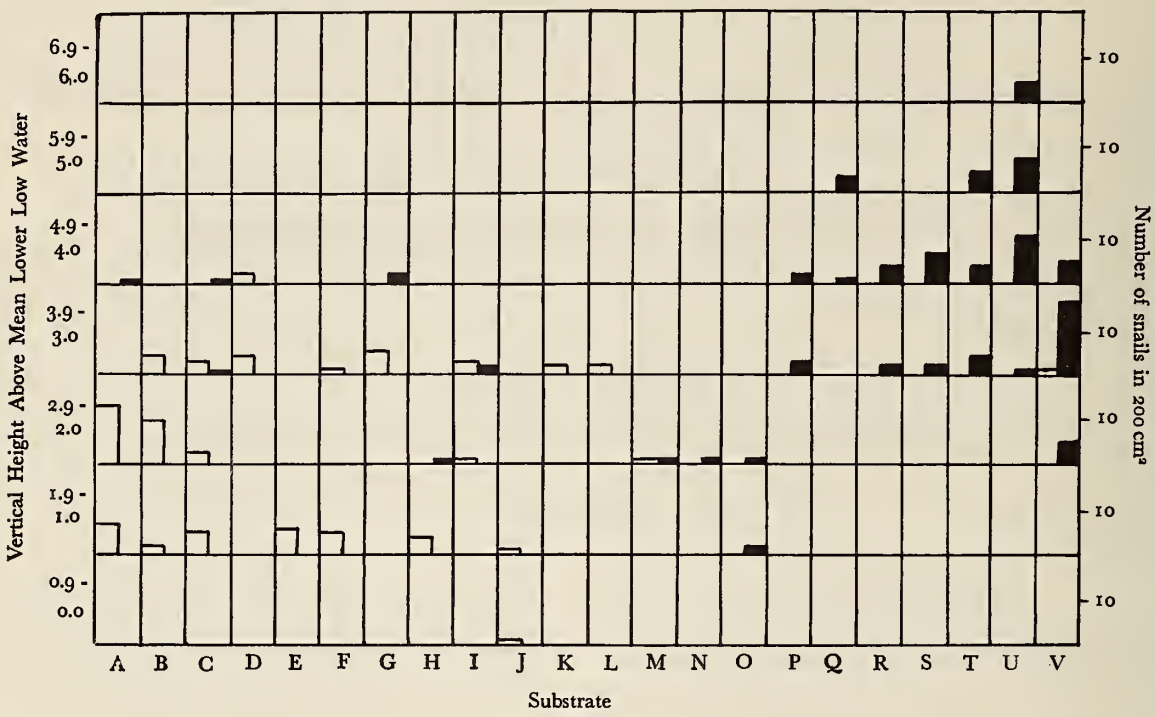

Figure 1

Low tide distribution of juvenile *Tegula funebralis* (white bars) and *Littorina scutulata* (black bars), based on pooled data from 4 transects at Mussel Point, Pacific Grove, California. Numbers indicate the numbers of snails taken from the various microhabitats at each level. Letters refer to the following microhabitats:

A. Sandy holdfasts of *Rhodoglossum affine*
B. Sandy holdfasts of *Gigartina papillata*
C. Rocky crevices
D. Sandy holdfasts of *Gigartina agardhii*
E. Crustose red algae
F. Sand
G. Sandy holdfasts of *Endocladia muricata*
H. Sandy holdfasts of *Gelidium* sp.
I. Rocky holdfasts of *Gigartina papillata*
J. Sandy holdfasts of *Gigartina leptorhynchos*
K. Rocky holdfasts of *Iridaea* sp.
L. Tidepools
M. Crustose coralline algae
N. Fronds of *Iridaea* sp.
O. Fronds of *Rhodoglossum affine*
P. *Pelvetia fastigiata*
Q. Rocky holdfasts of *Endocladia muricata*
R. Fronds of *Gigartina agardhii*
S. Fronds of *Endocladia muricata*
T. Bare Rock
U. Empty barnacle shells
V. Fronds of *Gigartina papillata*

Tegula funebralis complement and extend existing information on the distribution of the species. Seapy & Littler (1979) at Cayucos Point, California, determined the *T. funebralis* vertical population distribution to lie between 117 cm and 27 cm above MLLW. Wara & Wright (1964), working with the occurrence at low tide of specimens over 13 mm in length at Pacific Grove, found that the population density decreased as the amount of the algal cover on the substrate increased. The smaller animals tended to be higher up and farther inshore. In the present study, adults were more common at lower elevations; they occurred on relatively bare rock surfaces, whereas the juveniles were found in the sandy holdfasts of macroalgae. Juvenile *T. funebralis* were often commonly on the undersides of rocks in the pools—areas where the larger adults could not take refuge. However, specimens over 6 mm in diameter routinely occurred in the same crevices as the larger animals. The tendency toward habitat separation of juveniles from

larger animals should tend to reduce intraspecific competition, possibly important in a species where individuals may live as long as 30 years (Darby, 1964).

The studies of Chow (1975), on the distribution of *Littorina scutulata* at Bodega Head showed that individual size tends to increase with increasing vertical height in the intertidal zone, though juvenile (1-4 mm) snails occurred over the entire vertical range. Both the vertical range of the population (0.9-3.6 m above MLLW) and vertical position of the peak in population density (1.86 m) in Chow's study site were higher than those observed at Mussel Point, a difference very likely related to stronger surf at Bodega Head.

More recent studies by Murray (1979), reveal differences in egg mass shape and penis shape in adult *Littorina scutulata,* suggesting that two distinct forms or species may exist and even occur together on the West Coast. As only juvenile individuals were dealt with in my study, all *L. scutulata* were treated as a single population.

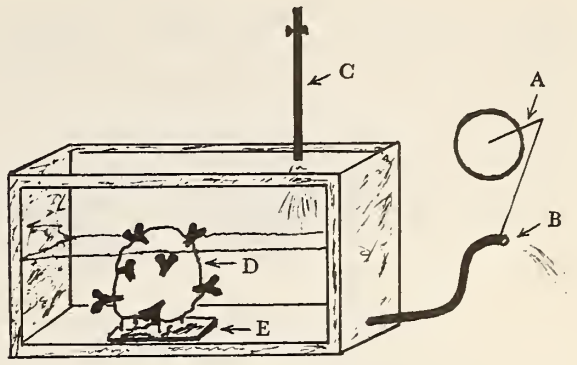

Figure 2

Aquarium used to simulate tidal conditions in the laboratory Hour hand of the clock (A) raises and lowers outflow hose of the aquarium (B). Seawater flow into tank (C) is constant. Rock simulating natural habitat (D) is supported above the bottom on slender pegs (E)

ACTIVITY

Although it was feasible to determine the vertical position and microhabitat distribution at low tide of juvenile *Tegula funebralis* and *Littorina scutulata,* it was desirable to supplement this with information on movements of the animals and their distribution at high tide. This proved difficult in the field even in a region of moderate surf. Thus, observations were made under laboratory conditions. An artificial tide was created in an aquarium with a constant inflow of seawater at 14-15° C. A clock was used to control water level; the tip of the outflow hose of the aquarium was attached to a rod extending from the hour hand of the clock (Figure 2), providing an approximately natural cycle of two high and two low tides each 24 hours.

A rock collected from the intertidal zone in an area common to both species and placed in the aquarium provided a natural habitat. This rock was visually divided into 3 vertical zones (high, middle, and low), each forming a belt 5 cm wide and each with approximately the same proportion of *Gigartina papillata* (C. Agardh) J. Agardh, 1846 and bare surface. A vertical crevice ran down one side of the rock. The artificial tide was adjusted so the rock was completely covered at high water and completely exposed at low water. A skylight over the aquarium in the laboratory provided a natural light regime.

To increase contrast between snails and background the experimental animals were marked with fingernail polish, distinctive colors being used for the two species. Twenty marked juveniles of each species were selected, placed on top of the rock in the aquarium, and allowed to move about and acclimate for 24 hours. Thereafter, at 2 hour intervals over a 24 hour tidal cycle, the number of snails of each species in each vertical zone on the rock (high, middle, low) and on each type of substrate (*Gigartina papillata* fronds, the lower frond/holdfast area, the rock surface, or the rock crevice) was recorded. A dim red light was used to make observations at night. Later the same experiment was repeated, but with the tidal clock shifted by six hours, yielding data under a different phase relationship of the diel and tidal cycles. The animals were allowed to adjust to the new tidal regime for 24 hours before observations of movement began.

The results of both experiments are shown in Figure 3. As regards vertical zonation on the rock, the *Littorina scutulata* population was found to occur higher than the *Tegula funebralis* population under all conditions of light and tide. The greatest overlap between the populations occurred on the middle region of the rock. The *T. funebralis* juveniles, however, displayed greater vertical mobility. Individuals often moved to the high surface of the rock as the water rose, and returned to the lower regions as it fell. When the receding tide occurred at night, fewer snails moved down, and as a result more were left high on the rock at the morning low tide. The large number of *Tegula* low on the rock at high tide in the dark is contrary to the general trend. Most of these snails, however, were active on the rock surface, and were observed moving up the

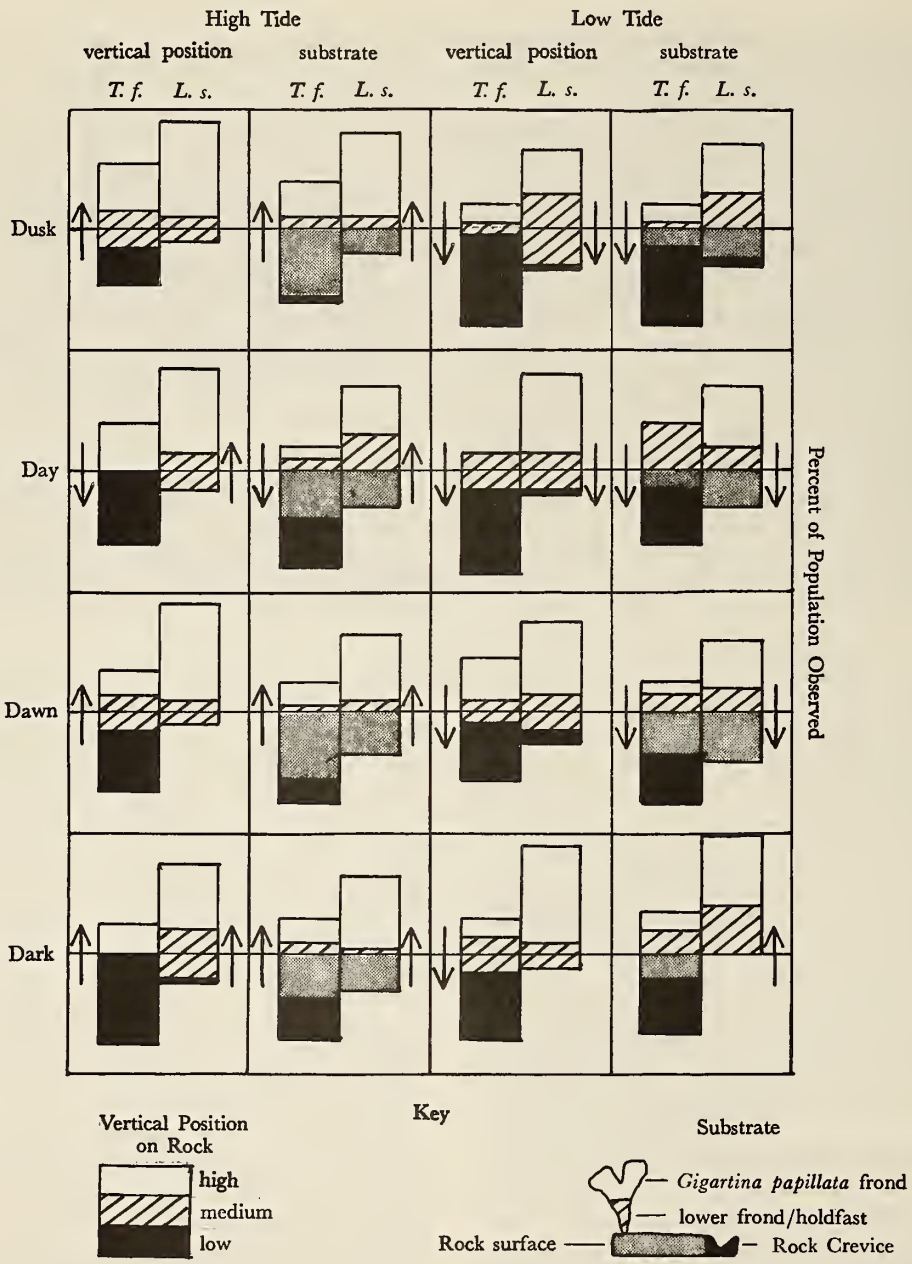

Figure 3

Vertical position and microhabitat choice of juvenile *Tegula funebralis* and *Littorina scutulata* on a rock in a laboratory aquarium, under varying conditions of light and tide. The bars indicate the percent of the population observed on the different substrates and at different elevations on the rock. Horizontal rows are arranged in the order of the number of snails of both species on the high zone of the rock at high tide; this number decreases from top to bottom of the graph. Arrows refer to the predominant movement of the populations during the two readings made prior to the condition shown; the left arrow in each column refers to *T. funebralis*, the right one to *L. scutulata*. Where no arrow appears, vertical shifts in the population of snails approached zero. With respect to vertical position, the mid-line represents the middle of the rock. The mid-line in the substrate columns divides snails on *Gigartina papillata* (above the line) from those on rock substrates (below the line)

rock. The *L. scutulata* juveniles showed a slight tendency to move downward on the rock during daylight falling tides. Snails of both species were observed moving away from direct sunlight when completely submerged during a daylight high tide. With regard to the specific substrates on which the animals were found, *Littorina scutulata* juveniles tended to remain on *Gigartina papillata,* moving to the tips of fronds when covered by water, while young *Tegula funebralis* were observed predominantly on the rock surface, retreating to the crevice, rock bottom and *G. papillata* holdfasts at low tide.

The separation of the two species observed under laboratory conditions correlates well with differences in zonation and microhabitat distribution presented in Figure 1. Juveniles of *Littorina scutulata* continue to occupy a higher zone than juvenile *Tegula funebralis,* despite compression of the 1.8 m vertical range found in the field into a 15 cm range in the laboratory tank. The habitat differences of the two species in the field at low tide persist through the tidal cycle; *Tegula funebralis* juveniles continue to be found mainly on the rock surface and *Gigartina papillata* holdfasts and young *Littorina scutulata* predominate on the *G. papillata* fronds. This continued occupancy of distinct microhabitats supports the idea of a real resource partitioning between juveniles of the two species.

Daniels (1978), studying the activity of adult *Tegula funebralis* under field and laboratory conditions, found that population movements corresponded to the tidal cycle. However, in the absence of tidal fluctuations (as in outdoor aquaria kept continuously full of water) movement occurred according to a diel cycle, with the animals moving up rock surfaces at night, and down to shaded areas in the day. He also observed adult *T. funebralis* occasionally left high and dry in the field after a receding tide at night, and concluded that light reinforces the downward response of the animals. In the present study, juvenile *T. funebralis* generally show these same tendencies, but the phototactic response of both adults and juveniles need further investigation.

FOOD HABITS

Juvenile snails of both species were collected from the field, usually during early morning low tides, when the animals—still wet from the previous high tide—had full stomachs. The substrate on which they were found was noted, and the animals were immediately preserved in 10 per cent formalin. In the laboratory the stomachs were removed under a dissecting microscope. Gut contents were mounted on slides in glycerol, and examined at 400X. Dr. Isabella A. Abbott and Mr. William Magruder assisted in the identification of possible food items. Materials in the gut were grouped into five categories: detritus (organic material of unidentifiable origin), green algae, diatoms, dinoflagellates, and other (miscellaneous). Relative abundance of the different constituents, as a percentage of the total biomass of the contents, was visually estimated.

Figure 4 shows the means and ranges of the categorized gut contents of 10 juveniles of each of the two species. Both

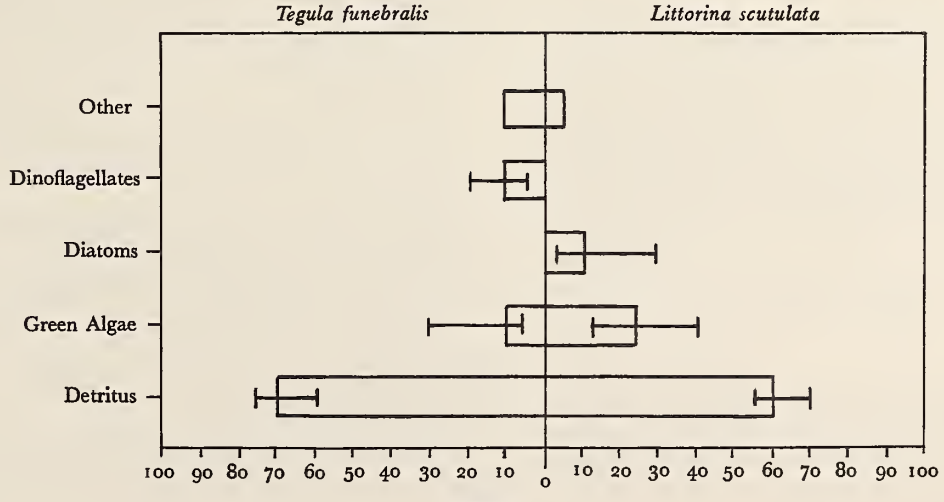

Figure 4

Diet of juvenile *Tegula funebralis* and *Littorina scutulata* as percentage of the total biomass of stomach contents. Bars shown are the averages based on 10 snails. Lines on the bars give the range

species contained much detritus. *Littorina scutulata* juveniles contained more green algae and diatoms than did juvenile *Tegula funebralis,* and the latter showed many small,brown dinoflagellates lacking in the gut of *L. scutulata.* A few cells from encrusting red algae and an occasional foraminiferan were found in the stomachs of small *T. funebralis.*

The high concentration of detritus in the guts of both species suggests that they feed in a similar and relatively non-selective manner. The higher percentage of green algae and diatoms consumed by young *Littorina scutulata* may reflect ingestion of epiphytes, for these are found on the macroalgal fronds frequented by the snails. I saw no evidence of feeding on any of the larger macroalgae, such as *Gigartina papillata* or *Rhodoglossum affine.*

Comparison of these results with the findings of Best (1964) indicate that the diets of adult and juvenile *Tegula funebralis* are quite different. Best found the adults fed on a variety of large and small algae, with detritus contributing little bulk. The amount of detritus consumed by juveniles in the present study again suggests a partitioning of resources between different stages in the life history.

The investigations of Dahl (1964) and Foster (1964) on the microscopic and macroscopic food sources of adult *Littorina scutulata* show that macroalgae, particularly *Pelvetia fastigiata* (J. Ag.) De Toni, 1895 and *Cladophora columbiana* Coll., 1903, were preferred food sources of snails in the laboratory, although green algae and diatoms contributed significantly. No indication of feeding on detritus was noted, but the stomach contents of animals freshly collected from the field were not examined. As in *Tegula funebralis,* the difference in food habits between juveniles and adults may enable larger populations to be supported.

Despite the similarity of the gut contents in juveniles of *Tegula funebralis* and *Littorina scutulata,* it appears likely that there is little interspecific competition for food. Both field and laboratory studies indicate that the species forage in relatively distinct subhabitats.

SUMMARY

At Mussel Point, Pacific Grove, California, juveniles (4 mm or less in greatest shell dimension) of *Tegula funebralis* and *Littorina scutulata* occupy largely separate microhabitats. At low tide, juveniles of *T. funebralis* occur predominantly in the sandy holdfasts of macroalgae and in rock crevices, less than 1.2 m above mean lower low water; juveniles of *L. scutulata* are found mainly on the fronds of macroalgae and in empty barnacle shells more than 0.9 m above MLLW. Laboratory experiments in aquaria with artificial tides demonstrate a similar partitioning of the habitat by vertical position and microenvironment.

Juveniles of both species appear to be mainly relatively non-selective detritivores. Young *Littorina scutulata* consume more green algae and diatoms, probably representing the ingestion of epiphytes; *Tegula funebralis* contained more dinoflagellates. While juveniles of the two species consume roughly the same food, they obtain it in different places, so competition appears light.

ACKNOWLEDGMENTS

I wish to thank the entire instructional staff of the Hopkins Marine Station for their help and encouragement throughout the course of this study. I am particularly indebted to Dr. Donald P. Abbott for helpful advice and guidance during all stages of the work.

Literature Cited

Abbott, Donald Putnam & Eugene Clinton Haderlie
1980. Prosobranchia: Marine Gastropoda. *In*: R. Morris, D. P. Abbott & E. C. Haderlie (eds.), Intertidal invertebrates of the California coast. Stanford Univ. Press, Stanford, Calif. xi+690 pp.; 200 plts. (November 1980)

Best, Barbara
1964. Feeding activities of *Tegula funebralis* (Mollusca : Gastropoda). The Veliger 6 (Supplement): 42 - 45; 1 text fig. (15 November 1964)

Chow, Victor
1975. The importance of size in the intertidal distribution of *Littorina scutulata* (Gastropoda : Prosobranchia). The Veliger 18 (1): 69 to 78; 8 text figs. (1 July 1975)

Dahl, Arthur Lyon
1964. Macroscopic algal foods of *Littorina planaxis* Philippi and *Littorina scutulata* Gould (Gastropoda : Prosobranchiata). The Veliger 7 (2): 139 - 143 (1 October 1964)

Daniels, Matthew
1978. Rhythmic movement of the marine snail *Tegula funebralis* (Prosobranchia: Trochacea) on intertidal rocks in relation to tidal and diel cycles. Unpubl. stud. reprt. on file at Hopkins Marine Station library, Pacific Grove, Calif.; 12 pp.

Darby, Richard L.
1964. On growth and longevity in *Tegula funebralis* (Mollusca : Gastropoda). The Veliger 6 (Supplement): 6 - 7; plt. 1 (15 Nov. '64)

Foster, Michael S.
1964. Microscopic algal food of *Littorina planaxis* Philippi and *Littorina scutulata* Gould (Gastropoda : Prosobranchiata). The Veliger 7 (2): 149 - 152, 152a (1 October 1964)

Murray, Talbot
1979. Evidence for an additional *Littorina* species and a summary of the reproductive biology of *Littorina* from California. The Veliger 21 (4): 469 - 474; 2 text figs. (1 April 1979)

Seapy, Roger R. & Mark M. Littler
1978. The distribution, abundance, community structure, and primary productivity of macroorganisms from two central California rocky intertidal habitats. Pacif. Sci. 32 (3): 293 - 314 (July 1979)

Wara, William M. & Benjamin B. Wright
1964. The distribution and movement of *Tegula funebralis* in the intertidal region of Monterey Bay, California (Mollusca : Gastropoda). The Veliger 6 (Supplement): 30 - 37; 9 text figs. (15 November 1964)